AN EXPERIMENTAL GRADIENT ANALYSIS: HYPOSALINITY AS AN "UPSTRESS" DISTRIBUTIONAL DETERMINANT FOR CARIBBEAN PORTUNID CRABS

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Gradients provide opportunities to examine the responses of populations to their environments, and their contributions to community structure. Interpreting observations from gradients is easiest when a single important physicochemical factor varies monotonically. When no major physicochemical variable is monotonic, two or more actual gradients result. For example, in North America, peak air temperatures decline both north and south from mid-continent maxima (MacArthur, 1972). Alternatively, when more than one major physicochemical variable is monotonic, as in the altitudinal gradients studied by Terborgh (1971) and Whittaker (1967), their effects cannot be unraveled by observation alone. Since many, perhaps all gradients are complex (those Whittaker, 1967, defined as having multiple physicochemical variables), experimental manipulations permit isolation of variables, greatly increasing the utility of gradient analyses.

This study examines some determinants of swimming crab distributions along gradients in terrestrial influence on aquatic climate having monotonically varying salinities. Most of the ~ 300 species in the family Portunidae inhabit shallow tropical marine waters (Rathbun, 1930; Stephenson, 1972), but crabs in the Indo-West Pacific genus *Scylla,* and the Atlantic and East Pacific genus *Callinectes,* inhabit climatically more rigorous biotopes, such as rivers and estuarine bays. The weather of waters in most portunids' habitats is less influenced by aerial weather over the nearest landmasses than is aquatic weather in the habitats of *Scylla* and *Callinectes.* We will focus on a functionally similar grouping, or guild (Root, 1967) of Caribbean species in the largest portunid subfamily, the Portuninae. The guild members are demersal, in and epifaunal carnivores or carnivore-detritivores with long-lived planktotrophic larvae. They had been studied mainly taxonomically, with the exception of *Callinectes sapidus* Rathbun, a commercial species which controls community structure of estuarine benthos in Chesapeake Bay, USA (Virnstein, 1977). *C. sapidus* occurs from fresh through marine and even hypersaline waters (Mangum and Amende, 1972; Simmons, 1957). It is catadromous; females migrate from hyposaline waters (having less than about 35‰ salinity) to higher salinities to spawn and hatch their eggs (Churchill, 1919; Van Engel, 1958). The planktonic early zoeal larvae are orthostenohaline (Kalber, 1970), while subsequent megalopae and crab stages, which reinvade estuaries, are progressively more euryhaline (Costlow, 1967; Tagatz, 1971).

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Scattered previous records (Coelho, 1965, 1967; Holthuis, 1959; Rouse, 1969; Taissoun, 1973) and inferences from geographic distributions (Norse, 1977) indicated that salinity is a major niche axis along which Caribbean portunid species are differentially distributed. For this originally marine group, rivers (in which salinities are constantly stressful) and nearshore shallows (where salinity stress is highly variable and unpredictable) should mark "upstress" ends of species' distributions, which extend through more equable waters to seaward. "Upstress" is the direction of increasing physiological stress directly attributable to physico-chemical change. Differential upstress limits for Caribbean portunids should there-fore reflect varying tolerances of hyposalinities. To test this, experiments in this study simulate acutely diluted conditions portunids can encounter in the study areas. Norse (1978) and Norse and Estevez (1977) considered some factors limiting portunids' "downstress" distributions.

Jamaica was the main study area for field and laboratory work. The number and extent of Jamaican hyposaline biotopes depend more on upland, than local rainfall; *e.g.*, the Martha Brae, one of the largest rivers, feeds a large brackish bay in one of the island's driest regions. Most work was done on the North Coast, where the shelf is narrow, and shallow soft bottoms suitable for most Caribbean portunids occur in relatively small pockets in which waters may grade from riverine to oceanic in a few hundred meters.

Supplemental field work was done in the Middle Florida Keys, USA, in 1972 and 1974, in Colombia between the Ciénaga Grande de Santa Marta and Bahía Concha in 1972, and in Curaçao in 1975. Descriptions of sites in Jamaica, Colombia and the Florida Keys appear in Norse (1975).

MATERIALS AND METHODS

Distributions

Crabs were sampled in coastal and lotic waters by trapping, hand-netting and gill-netting. To minimize bias, crabs were hand-netted in the order in which they were spotted.

Thirty-two Jamaican quantitative sites were sampled from 1 to 13 times in July to August, 1970 and May to October, 1972. Crabs were sorted to species and sex and measured (carapace length, CL, along midline) immediately after capture. Water samples were taken just above the substratum in the middle of collecting sites. Most salinities were measured with an American Optical salinity model refractometer to the nearest $\frac{1}{2}$‰; a few were determined by titration. Sup-plemental collections included those in which crabs from adjacent habitats were pooled, less than five crabs were taken, or particular species, sexes or sizes were sought for experiments.

Hyposalinity tolerances

Jamaican *Callinectes maracaiboensis* Taissoun, *C. bocourti* A. Milne Edwards, *C. sapidus*, *C. exasperatus* (Gerstaecker), *C. danae* Smith, *C. marginatus* (A. Milne Edwards), *C. ornatus* Ordway, *Arenaeus cribrarius* (Lamarck) and *Portunus sebae* (H. Milne Edwards) were brought to Discovery Bay Marine

Laboratory in 1972. Although aware that Taissoun (1972) was describing a new species (*C. maracaiboensis*), I was unaware that its range included Jamaica (see Norse, 1977), and unfortunately, did not distinguish it from the morphologically very similar *C. bocourti* in any laboratory experiments. For convenience, they will be referred to as "*C. bocourti*" where appropriate. Crabs collected below 20‰ were placed in stepwise increasing salinities for several hours. All were acclimated in running seawater (salinity unvaryingly 34.5‰; mean temperature 28.9° C) for a minimum of 30 hr. Healthy hard-shelled crabs were placed singly into covered, individually aerated plastic buckets containing 1 to 3 liters (according to crab size) of water prepared by diluting 100% seawater with unchlorinated tapwater to 50, 25, and 10% seawater concentrations. Salinities were measured and adjusted where necessary. Three hundred eighty crabs were tested, and after 24 hours, examined for survival. "Living" crabs moved appendages and responded to prodding, although some were obviously stressed and probably would not have survived continued dilution.

Further experiments were done in the Florida Keys in July, 1974 at Pigeon Key Marine Environmental Station. *Callinectes ornatus, Portunus depressifrons* (Stimpson), *P. spinimanus* Latreille, *P. gibbesii* (Stimpson) and *Cronius tumidulus* (Stimpson) were collected near Ohio (= Sunshine) and Missouri Keys. Acclimation salinities averaged 36.3‰ and varied no more than 1‰ from this value; temperatures averaged 27.9° C. This time, crabs were placed in 1 liter of seawater diluted with aged tapwater to 50, 37.5, and 25% seawater concentrations; 264 were tested. Experiments were otherwise similar to those in Jamaica.

RESULTS

Distributions

A total of 943 *Callinectes* belonging to eight species, and 47 other demersal portunids (five species) were collected in Jamaican quantitative samples; hundreds more belonging to 16 species were observed or collected at supplemental sites in Jamaica, Florida, Colombia and Curaçao. Two previously unrecorded species were found in Jamaica; *C. maracaiboensis* is common there (Norse, 1977), while *C. similis* Williams (3 individuals) was taken only once.

All guild members occur in marine salinities, although progressively fewer species were found as salinities decreased. Table I gives the highest and lowest salinity records (ecological amplitude—Terborgh, 1971), and the highest and lowest mean salinities of quantitative sites where each Jamaican species comprised ≥ 25% of the portunids taken, an arbitrary measure of ecological importance. *Callinectes maracaiboensis, C. bocourti, C. sapidus* and *C. exasperatus* have ecological amplitudes exceeding 33‰, while *C. danae, C. marginatus, C. ornatus, Arenaeus cribrarius* and the others have progressively smaller ones, although *A. cribrarius* and the others were found at two or fewer Jamaican sites. *C. sapidus* is ecologically important over a range of 23.9‰; diminishing ranges are seen for *C. maracaiboensis* (21.3‰), *C. bocourti* and *C. exasperatus* (19.8‰), *C. danae* (14.3‰), *C. marginatus* (8.5‰), *C. ornatus* (3.4‰) and *P. sebae* (0.0‰).

Table I also gives the means of indivdual site species compositions (dominance) for *Callinectes* in four salinity categories: "freshwater" (actually including

TABLE I

Salinity distributions of Jamaican portunids (C. represents Callinectes). Ranges of occurrence and of ecological importance (in ‰).

	Lowest	Lowest $\bar{X}$ where sp. $\geq 25\%$	Highest $\bar{X}$ where sp. $\geq 25\%$	Highest
C. maracaiboensis	0.0	0.5	21.8	35.0
C. bocourti	0.0	2.0	21.8	34.5
C. sapidus	0.0	0.5	24.4	34.5
C. exasperatus	2.0	15.5	35.3	35.5
C. danae	11.0	17.8	32.1	34.6
C. marginatus	15.0	26.8	35.5	35.5
C. ornatus	17.8	32.1	35.5	35.5
C. similis	34.5			34.5
Portunus sebae	34.5	34.5	34.5	35.3
P. anceps	34.5			35.5
P. depressifrons	34.5			34.5
Arenaeus cribrarius	30.5			34.5
Cronius tumidulus	34.5			34.5

Callinectes spp: dominance (relative abundances of species (in per cent) in 4 salinity categories; Σ each category = 100%).

	0–10.0‰	10.1–30.0‰	30.1–33.0‰	33.1–35.5‰
C. maracaiboensis	41.0	10.0	4.0	0.4
C. bocourti	34.5	10.4	0.4	0.7
C. sapidus	22.5	15.2	4.6	1.5
C. exasperatus	2.0	29.6	22.8	27.5
C. danae	0.0	16.0	23.1	1.9
C. marginatus	0.0	16.6	30.9	29.5
C. ornatus	0.0	2.4	14.2	38.0
C. similis	0.0	0.0	0.0	0.2

the lower brackish range, 0–10.0‰), "brackish" (10.1–30.0‰), "near-marine" (30.1–33.0‰) and "marine" (33.1–35.5‰). Freshwater sites are dominated by *C. maracaiboensis, C. bocourti* and *C. sapidus,* brackish sites by *C. exasperatus,* near-marine sites by *C. marginatus, C. danae* and *C. exasperatus,* and marine sites by *C. ornatus, C. marginatus* and *C. exasperatus.*

In Jamaica, males comprised 12/16 (75%) of the *C. sapidus* adults in salinities below 15‰, but only 6/29 (21%) of the adults in higher salinities. This difference is highly significant ($G_{adj} = 10.7$; $P < 0.005$). Analogous patterns were seen in the other Jamaican freshwater species, *C. maracaiboensis* (16/20 vs. 2/21; $G_{adj} = 19.6$; $P << 0.001$) and *C. bocourti* (13/16 vs 1/11; $G_{adj} = 11.8$; $P < 0.001$). Among the three freshwater species, none of the 11 adult females taken below 15‰ was ovigerous, while 7/52 (13%) in higher salinities bore egg sponges. None of the 19 ovigerous females in other Jamaican *Callinectes* occurred below 15‰. Like North Temperate *C. sapidus* populations, Jamaican *Callinectes* appear unable to reproduce in low salinities, and the freshwater species are catadromous, storing energy in low salinity ecosystems but spawning and hatching their eggs in higher salinities.

TABLE II

Hyposalinity tolerances of Jamaican portunids.

	# tested	% surviving
Transfers from Discovery Bay seawater (34.5‰) to 10% seawater		
"*Callinectes bocourti*"	24	100
C. sapidus	20	100
C. exasperatus	33	88
C. danae	36	50
C. marginatus	29	7
C. ornatus	36	3
Transfers to 25% seawater*		
C. marginatus	30	67
C. ornatus	45	22
Arenaeus cribrarius	6	0
Portunus sebae	6	0
Transfers to 50% seawater*		
C. ornatus	21	100
A. cribrarius	6	83
P. sebae	6	17

* "*C. bocourti*," *C. sapidus*, *C. exasperatus*, and *C. danae* (25% seawater) and *C. marginatus* (50% seawater) had 94 to 100% survival.

Hyposalinity tolerances

Table II shows survival of Jamaican portunids transferred from seawater to diluted seawater. There are marked differences among *Callinectes* transferred to 10% seawater (G-test for heterogeneity, $G_H = 148.2$ with 5 df; $P << 0.001$). Using the conservative STP *a posteriori* test procedure (Sokal and Rohlf, 1969), "*C. bocourti*" (including *C. maracaiboensis*) and *C. sapidus* are not significantly more tolerant than *C. exasperatus*, but *C. exasperatus* is significantly more tolerant than *C. danae* ($G_H = 12.2$; $P < 0.05$), *C. danae* is significantly more tolerant than *C. marginatus* ($G_H = 15.8$; $P < 0.01$), and differences between *C. marginatus* and *C. ornatus* are not significant. Transfers to 25% seawater show marked differences among *C. marginatus, C. ornatus, Arenaeus cribrarius* and *Portunus sebae* ($G_H = 26.2$ with 3 df; $P << 0.001$). *C. marginatus* is significantly more tolerant than *C. ornatus* ($G_H = 15.1$; $P < 0.005$), but *C. ornatus* is not significantly more so than the others. Transfers to 50% seawater also show marked species' differences ($G_H = 20.5$ with 2 df; $P << 0.001$). Two groupings, within which differences are not significant at $P = 0.05$, are: *C. ornatus* with *A. cribrarius* and *A. cribrarius* with *P. sebae*.

The lowest salinities in which the common Jamaican *Callinectes* occur, or are ecologically important (at least 25% of the congeners at the site) are very highly correlated ($P < .001$ for both) with their hyposalinity tolerances (Fig. 1).

Table III shows survival of Florida Keys crabs subjected to diluted seawater. There are marked differences among the species ($G_H = 70.2$ with 4 df; $P << 0.001$) in transfers to 25% seawater, with *C. ornatus* more euryhaline than the others. Neither sexes nor sizes of *C. ornatus* differ significantly, nor do *Portunus*
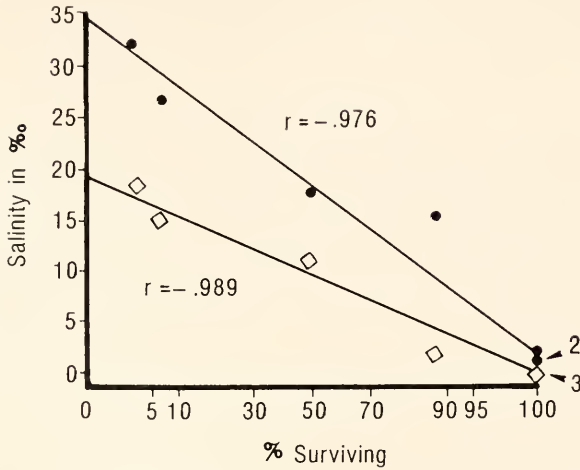
FIGURE 1. Relationship of hyposalinity tolerance (survival when transferred from seawater to 10% seawater) to lowest salinity (diamonds) and lowest salinity of ecological importance (circles) for seven common Jamaican *Callinectes* spp.

depressifrons and *P. spinimanus* when transferred to 37.5% seawater. When transferred to 25% seawater, Florida Keys *C. ornatus* are significantly more tolerant than Jamaican conspecifics ($G_{adj} = 18.0$; $P << 0.001$). In transfers to 50%

TABLE III

Hyposalinity tolerances of Florida Keys portunids.

	# tested	% surviving
Transfers from Pigeon Key seawater (36.3‰) to 25% seawater		
Callinectes ornatus	87	62
Males	53	62
Females	32	63
Sacculinized crabs	2	50
Larger crabs (>24 mm)	42	71
Smaller crabs (≤24 mm)	45	53
Portunus depressifrons	23	0
P. spinimanus	23	0
P. gibbesii	2	0
Cronius tumidulus	4	0
Transfers to 37.5% seawater		
Callinectes ornatus	18	100
P. depressifrons	30	30
P. spinimanus	21	14
Transfers to 50% seawater*		
P. depressifrons	9	100
P. spinimanus	15	100

* *C. ornatus* (50% seawater) had 100% survival.

seawater. Keys *P. depressifrons* and *P. spinimanus* are significantly more euryhaline than Jamaican *P. sebae* ($G_H = 27.0$ with 2 df; $P << 0.001$).

DISCUSSION

Caribbean portunids show serial replacement along gradients in terrestrial influence on aquatic climate. All 16 portunid species that were collected occur in undiluted seawater, but *Callinectes* virtually monopolize hyposaline biotopes. None of the ~ 290 *Portunus* or *Cronius* was found in hyposaline water, and *Arenaeus cribrarius* was taken at salinities no lower than 87% seawater. In contrast, all common Jamaican *Callinectes* occur down to 50% seawater or less. These generic distributional differences reflect differing hyposalinity tolerances. Pearse (1929) found that two *Portunus* spp. are less dilution-tolerant than *C. marginatus,* and none of the six *Portunus, Cronius* and *Arenaeus* species tested in the present study appears to tolerate acute seawater dilution as well as the least euryhaline *Callinectes.* Similar portunid distribution sequences occur along salinity gradients in the East Pacific off Colombia (Norse and Estevez, 1977). Euryhalinity permits American *Callinectes* to exploit resources in physicochemically harsh, but highly productive ecosystems from which other, potentially competing portunids (and other marine taxa) are absent.

The four to five levels of euryhalinity evolved by Caribbean *Callinectes* are strikingly correlated with species' penetration into hyposaline waters (Fig. 1). This strongly suggests a causal relationship, but does not distinguish the nature of the underlying mechanism, as Wolcott (1973) noted in his study on limpets. Upstress distributions may be directly extrinsically limited (through stress-induced death) or indirectly extrinsically limited (through death from stress-related failure to find, handle or assimilate food, escape damage in agonistic contests, evade predators or cope with parasites). Or, they may be intrinsically limited, through avoidance of low salinities.

Upstress limits may be determined by either usual or unusual weather. Available evidence indicates the latter. The extent and permanence of hyposaline biotopes differs among the study areas. Jamaica and the Ciénaga Grande de Santa Marta region in Colombia have numerous large hyposaline biotopes, while the Florida Keys, Curaçao and the area near the Colombian city of Santa Marta do not. Since rainfall in all these localities can be very intense, biotopes usually having marine salinities can undergo rapid, severe dilution. In general, likelihood and severity of dilution increase with increasing enclosure by land and decreasing depth and distance from shore. Thus, although the study areas are differentially endowed with permanent hyposaline biotopes, rapid salinity decreases can follow rains at sites in all.

Although *Portunus* were taken only in normally marine biotopes, environmental likelihood of severe dilution and euryhalinity are correlated among the species. In the Keys and Jamaica, *P. sebae* is the dominant portunid among lagoonal patch reefs and deeper, larger reefs in depths of 2 to 15 m (once at 76 cm). *P. depressifrons* in the same areas, and *P. spinimanus* in the Keys and Colombia, are common in the shallows (0–30 cm), often with *Callinectes marginatus* and *C. ornatus.* Similarly, although *P. sebae* occurs in Biscayne Bay, Florida, Park

(1969) found none in his shallow samples, which included *P. spinimanus* and hundreds of *P. depressifrons* and *C. ornatus*. *P. sebae* is less dilution-tolerant than these *Portunus* and *Callinectes*, and would seldom or never encounter substantial dilution in lagoon and fore reef ecosystems, while the others often would be subjected to mild, and occasionally severe dilution.

Another way to assess the effects of usual and unusual weather on distributions is to examine the physiology of whole assemblages. A measure of tolerance for each species can be multiplied by the species' ecological importance, and the products for all species added, yielding a weighted physiological index which can be plotted against a physicochemical variable. Unlike Whittaker's (1956), the method given below is not circular in assigning tolerances to species. A euryhalinity index (EI) for *Callinectes* (excluding *C. similis,* which is rare in Jamaica, and whose tolerances were not tested) at each site,

$$100 \sum_{i=1}^{7} AB$$

where A is the proportion of species *i* surviving transfer from seawater to 10% seawater and B is relative abundance (dominance) of species *i*, is plotted against mean salinity at 31 Jamaican sites in Figure 2. Clearly, low salinity assemblages are dominated by highly euryhaline species while less euryhaline species increasingly dominate as salinity increases, but there is also a mean-variance correlation, necessitating transformation of EIs before measurement of correlation is valid.
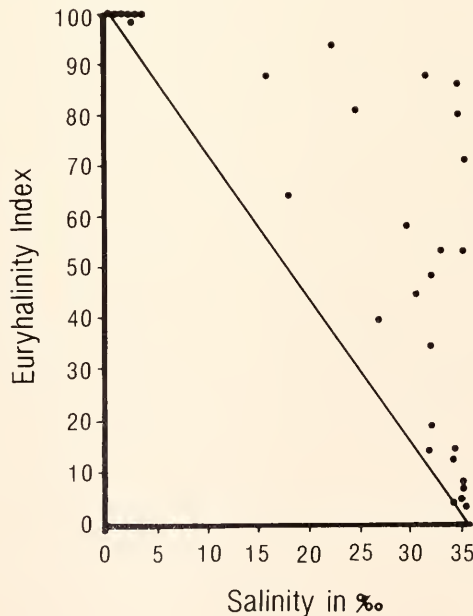

FIGURE 2. Weighted euryhalinity indices for *Callinectes* spp. at 31 Jamaican sites. The diagonal line estimates the euryhalinity indices of hypothetical sites with unvarying salinities.

Mean salinity and $\log_{10}$ (100-EI) are very highly correlated (r = 0.926 with 29 df; $P << 0.001$). Hence, 86% of the variation in EIs is explained by salinity. But what causes the increasing variability in untransformed EIs with increasing mean salinity? Apparently it is differential likelihood of severe dilution among sites having equal modal salinities.

Likelihood of severe dilution can be estimated without circularity (in this case, without using knowledge of portunids' tolerances) by using the previously discussed criteria (degree of enclosure, depth and distance from shore), non-portunid indicator species and published records. Jackson (1972) found rather constant salinities in eastern Discovery Bay (Site 16), while Taylor, Seliger, Fastie and McElroy (1966) found highly variable salinities in eastern Falmouth Bay (Site 9). I ranked the 11 Jamaican marine sites in Figure 2: Site 12 (the least variable, 1); 1 = 5 = 6 = 13 = 16 (all 4); 4 = 21 (both 7.5); 3 (9); 31 (10) and 9 (the most variable, 11). These ranks are highly correlated with ranked EIs (Spearman's $r_s = 0.808$; $P < 0.005$). Thus, in low salinities, variance among euryhalinity indices is small because conditions are constantly harsh, *i.e.*, always severely diluted. As usual conditions become less harsh, the variance among sites increases because EIs increasingly reflect likelihood of severe, rather than modal weather.

Similar patterns occur in regions lacking permanent hyposaline biotopes. In Curaçao, in one of the Schottegat's back bays (just W of Rijkseenheid Boulevard, N of Fokker Weg) about 3.3 km from the Caribbean, the estimated species composition was *C. maracaiboensis* (0.45), *C. exasperatus* (0.45) and *C. bocourti* (0.10). Using physiological data from Jamaican crabs, this assemblage can be estimated to have a euryhalinity index of 94.6. In the Waaigat, a blind channel communicating with the sea about 750 m distant through the narrow mouth of the Schottegat, the estimated species composition was *C. danae* (0.65), *C. exasperatus* (0.20), *C. marginatus* (0.13) and *C. ornatus* (0.02) (EI = 51.0). In the Caribbean at the Avila Beach Hotel, only *C. marginatus* was taken or observed (EI = 6.9). A line in Figure 2, on or above which are EIs for all Jamaican sites, estimates the salinities of hypothetical, climatically unvarying sites having equivalent EIs. The typically marine, but dilution-prone Schottegat back bay has a species composition that would be expected in a constant 2‰, while the progressively less variable Waaigat and Avila Beach Hotel sites have assemblages that would be expected in constant salinities of 17 and 33‰, respectively. Observations from the semiarid area near Santa Marta, Colombia present much the same picture. Thus, in biotopes lacking permanent freshwater input, the euryhalinity of the demersal crab guild is inversely proportional to the amount of exchange with the sea.

Boesch (1977) also found that benthic infauna in the poikilohaline Brisbane River, Australia, are limited by minimum salinities, which is not surprising considering their limited motility. But the findings above imply that swimming crabs do not move in response to changes in weather, which is surprising in view of vigorous escape movements and spawning migrations in various species. Since other fully aquatic decapods select salinities in experimental haloclines (Keiser and Aldrich, 1976), and *C. sapidus* has similar behaviors (along thermal gradients; Hoberg, 1975), Caribbean portunids would seem to have the kinds of behaviors

necessary to track suitable salinities. Indeed, one observation shows that *Callinectes* do move in response to changes in weather.

A small Jamaican stream, the Laughlands Little River, was flowing strongly in May (before quantitative sampling began) and early June, 1972; bottom salinities were $1\frac{1}{2}$, 2, and 0‰ during three visits. *C. maracaiboensis, C. bocourti* and *C. sapidus* were active in the stream. From late June through September, flow was much reduced, and bottom salinities were 23 to 33‰. Traps produced not only the freshwater species, but *C. exasperatus* and *C. marginatus,* which had invaded the stream from more saline areas. In this stream, even during a rainstorm, equable salinities would be only a few meters to seaward, but in most other biotopes sampled in this study, crabs would have to travel hundreds or thousands of meters to tolerable salinities, increasing the chance that they would be "trapped" while escaping.

Existing data showing that *Callinectes* both remain in, and leave environments during short-term salinity changes are not contradictory, but are a function of distance from waters with more stable salinity regimes. Since crabs escaping from low salinities can reinvade when salinities increase, but crabs which fail to cannot, the density of potential reinvaders in adjacent equable waters should decrease as the size of the stressed patch increases, decreasing the reinvasion rate. This rate should also decrease with increasing patch size because immigration is proportional to perimeter size, which increases less rapidly than area. In other words, populations of less euryhaline crabs invading increasingly large or remote, temporarily habitable biotopes should approach carrying capacity more slowly, because these biotopes are more difficult to leave and enter.

The high correlation between climatic variability and EI among sites with marine modal salinities is understandable if recolonization is not immediate. After severe dilution differentially defaunates a biotope, reestablishment of a later secondary successional stage (*sensu* Horn, 1974) requires a predictable amount of time unless another disturbance sets the process back. Climatically stable sites have sufficient disturbance-free intervals to develop climax community structures, but disturbance-prone sites are temporally dominated by disequilibrium species. This agrees with conclusions in a recent study of temperate infauna by McCall (1977).

The similar salinity zonation patterns throughout the Tropical West Atlantic imply consistent ranking of species' hyposalinity tolerances, but substantial quantitative differences were found between hyposalinity tolerances of Jamaican and Florida Keys *C. ornatus*. One possible explanation concerns differences in test conditions. The most likely are the slightly higher salinities in Keys experiments. Differing long-term acclimation effects offer another possible explanation. Keys crabs came from passes between islands, which have somewhat variable weather due to tidal alternation between Florida Bay and Atlantic water masses. A third possibility is that of genetic differences. Either the most stenohaline individuals are selected out from cohorts settling in the Keys (if Caribbean *C. ornatus* are panmictic), or Keys crabs are sufficiently genetically isolated to permit adaptation to local conditions. Differences in osmoregulatory ability have been shown in two European *Carcinus maenas* (Linnaeus) populations (Theede, 1969), but we

need to learn something of population genetics and larval dispersal in *Callinectes* before these differences can be explained.

Summary

This study examines ecological distributions in a guild of Caribbean demersal crabs (family Portunidae) on a gradient in terrestrial influence on aquatic climate, along which the major monotonic physicochemical variable is salinity. Distributions were established by sampling in fresh lotic waters and bays with highly restricted exchange with the sea, which, for marine groups, are constantly and unpredictably climatically severe, respectively, through climatically equable waters around coral reefs. The 16 demersal portunid species collected in Jamaica (the main study area), the Florida Keys, Colombia and Curaçao all occur in undiluted seawater, but progressively fewer are found as salinity decreases. Hyposaline biotopes are virtually monopolized by members of the genus *Callinectes*, while *Arenaeus*, *Portunus* and *Cronius* spp. were found only in higher salinities. *Callinectes* spp. display serial replacement along the gradient; crab stages of *C. maracaiboensis*, *C. bocourti* and *C. sapidus* occur mainly in fresh waters, while dominance peaks occur in progressively higher salinities for *C. exasperatus*, *C. danae*, *C. marginatus* and *C. ornatus*. Acute hyposalinity tolerances of the common species were determined experimentally, and follow the same order as upstress limits and dominance peaks. The species composition of the guild changes from domination by the most to the least euryhaline species as likelihood of severe dilution decreases. In biotopes with temporarily ameliorated weather, less euryhaline species invade and may replace more euryhaline species at a rate proportional to the biotope's remoteness from the immigrants' source area. Freshwater *Callinectes* are catadromous, storing energy in hyposaline ecosystems, but reproducing in higher salinities.

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